



RESEARCH ARTICLE

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Identifying Ecological Knowledge and Research Gaps via the African Database of Savanna Protected Areas (ADSPA)

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ABSTRACT

Aim: Despite their extent (40° of latitude and 50° of longitude), research in African savannas is dominated by a few heavily studied areas. We gathered data from African savanna protected areas to (i) evaluate their contributions to the primary literature, (ii) identify environmental groupings with respect to climate, soils, and landscape variables, and (iii) analyze the determinants of tree cover and fire within groupings.

Location: Africa.

Methods: We extracted climate, soil, topography, hydrology, elephant, fire, and tree cover data from polygon boundaries for 244 African savanna protected areas. The polygon layers and data were assembled into a novel geodatabase: African Database of Savanna Protected Areas (ADSPA). Cluster analysis identified natural bioclimatic groupings and structural equation modelling was used to analyse and compare the drivers of fire and tree cover within and across clusters.

Results: Previous literature disproportionately focused on a few savannas: 46% of savanna publications came from 2% of protected areas. Cluster analysis identified five bioclimatic groups: (1) African hot mesic savannas, (2) African cool mesic fertile savannas, (3) West African hot semi-arid savannas, (4) Southern African semi-arid savannas, and (5) Kalahari arid savannas. Current savanna science in protected areas is biased toward the Southern African semi-arid and African cool mesic fertile

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savannas, while hot mesic, hot semi-arid, and arid savannas are underrepresented. Climate and soils were strongly associated with tree cover and fire across protected areas, but no significant biome-wide effects of fire on tree cover emerged. However, tree cover was negatively related to fire in the hot mesic savanna cluster.

Main Conclusions: Significant biogeographic and ecological variation within African savannas highlights the need for research across the entire breadth of the biome, especially West Africa. We stress the need for spatially explicit, Africa-wide, data on mammalian herbivore biomass to better assess the importance of this variable for savanna functioning.

1 | Introduction

Savannas account for a large fraction of terrestrial biomes, including > 25% globally and > 50% in Africa (Ramankutty and Foley 1999; Strömberg and Staver 2022). Savannas have a heterogeneous tree layer over a grassy herbaceous layer (Ratnam et al. 2011); understanding what controls the coexistence of these two plant functional types has been of interest for decades (e.g., Bond 2008; Holdo and Nippert 2022). Globally, the spatial distribution of savannas is determined by climate factors, including rainfall and seasonality, and by dynamic disturbances, such as fire (Bond 2005; Lehmann et al. 2011; Staver et al. 2011). These grass-dominated ecosystems support a diverse range of large mammalian consumers (Hempson et al. 2015; Archibald and Hempson 2016) and are therefore crucial to the future of ungulate populations and important in global biogeochemical cycles, including carbon (Dobson et al. 2022). On the African continent, protected areas that restrict human settlement and land use represent the last refugia for natural vegetation (e.g., Smit et al. 2024), threatened and endangered large herbivores (e.g., Ripple et al. 2015) and carnivores (e.g., Riggio et al. 2013).

Woody encroachment threatens savannas globally (Stevens et al. 2017), and this may be intensified by tree planting initiatives to sequester carbon in arid lands (Lewis et al. 2019; Bastin et al. 2019), which may threaten the integrity of what would be grass-dominated habitats (e.g., Griffith et al. 2017; Veldman et al. 2019). Across Africa, Australia, and South America, woody biomass in savannas is controlled by climate (temperature and moisture), soils (texture and organic carbon), fire, and herbivory, but drivers differ among continents (Lehmann et al. 2014; Hempson et al. 2019; Staver et al. 2021), with implications for how vegetation might respond to climate change (Lehmann et al. 2014).

Within Africa, long-term research on savannas in Africa has been dominated by work in high-profile protected areas, such as Lamto Research Reserve in Cote d'Ivoire, the Serengeti–Mara ecosystem in Tanzania and Kenya, and Kruger National Park, Nylsvley Nature Reserve, and Hluhluwe–iMfolozi Park in South Africa (Figure 1A), representing much of the science on the functioning of African savanna ecosystems (e.g., Scholes and Walker 1993; Sinclair and Norton-Griffiths 1979; Du Toit et al. 2003; Abbadié et al. 2006). Historically, these research communities seldom integrated models or data from other regions (e.g., Chave et al. 2019). While extraordinary research has been undertaken in these areas, the first goal of this study is to quantify the extent to which current research represents the diversity and range of savanna ecosystems in Africa. In other words, is ecological variation across the African savanna biome well represented by published research, or does it tend to emerge from a limited number of areas? If the published literature represents narrow, or even redundant, portions of the African savanna biome, there may exist gaps in our understanding

of broad controls of tree cover, fire, and herbivory that limit future conservation efforts and capacity to make decisions in the face of global climate change (Aleman et al. 2020). Achieving this goal may enhance conservation and help ecologists focus and prioritise their research across the African continent into the future.

Analyses of vegetation patterns across Africa have separated savannas according to precipitation, soil fertility, leaf type, and type of herbivore defence (e.g., White 1983; Wigley et al. 2018). Recent analyses of woody plant species composition (e.g., Fayolle et al. 2019) found sites grouped according to a north-west/southeast dividing line (i.e., ‘White’s line’, White 1983) that split the continent into ‘High Africa’ in the south and east and ‘Low Africa’ in the north and west. Within these two broad groups, woody plant composition has been differentiated further into eight groups (two in the northwest and six in the southeast) with strong regional affiliation related to climate and elevation (Fayolle et al. 2019; Davies et al. 2023) that matched earlier bioregionalizations of Africa (e.g., Linder et al. 2012; Droissart et al. 2018). However, beyond classifications based on vegetation, defining natural climate, environmental, and landscape groupings may help conservationists focused on protected areas manage a broader range of species in the face of impending climate change. Consequently, the second goal of this study is to identify natural groupings of protected savanna areas across Africa as defined by their ecological and environmental properties, such as climate, soils, wetland area, tree cover and frequency of fires.

Finally, our third goal was to ask: within the best-supported natural groupings across African savannas, how do the relationships among environmental variables, fire, and tree cover vary in strength and identity? Other studies (e.g., Bucini and Hanan 2007; Sankaran et al. 2008; Lehmann et al. 2014) fit models to continental-scale data to describe the functional drivers of tree cover, but we ask: how consistent are the drivers of savanna structure across different regions of Africa? For example, regions of Africa with different compositions of the dominant vegetation (i.e., fine-leaved vs. broad-leaved woodland), may experience different controls on vegetation structure or disturbance (e.g., Osborne et al. 2018).

Here we present a novel database of 244 protected areas spanning the savanna biome of Africa across 31 countries. To address our first goal, we conducted a literature search of protected areas to understand their representation in the literature. To address our second goal, we analysed key biophysical properties of these protected areas, including climate, soils, topographic heterogeneity, and wetland area, and statistically grouped the data to map the spatial distribution of clusters. To address our third goal we analysed structural equation models to assess variation among regions of the African savanna biome. We hypothesized that soil, climate, landscape variables, fire, and elephants

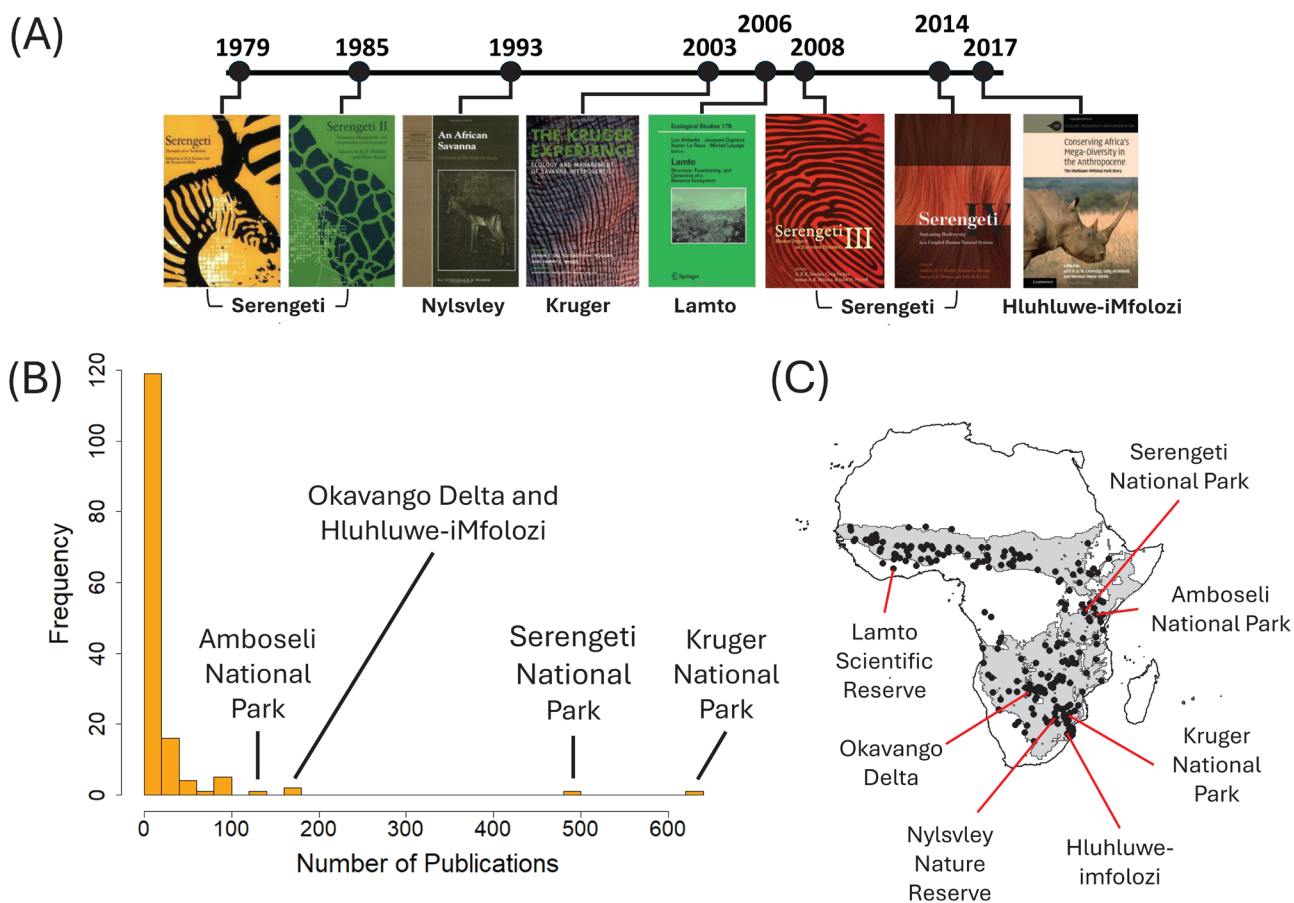


FIGURE 1 | Protected areas and research efforts within the African savanna biome. (A) Covers of edited volumes associated with long-term African savanna research areas (Serengeti National Park, Nylsvley Nature Reserve, Kruger National Park, Lamto Scientific Reserve, and Hluhluwe-iMfolozi Park) shown on a timeline with year of publication. (B) Publication frequencies of protected areas included in the African Database of Savanna Protected Areas (ADSPA) demonstrating disproportionate representation of Kruger in South Africa ($n=635$), Serengeti in Tanzania ($n=499$), Okavango Delta in Botswana ($n=173$), Hluhluwe-iMfolozi in South Africa ($n=168$), and Amboseli National Park in Kenya ($n=122$); the remaining areas had 92 or fewer publications. (C) Locations of 244 protected areas in ADSPA on a map of Africa with the seven well-studied areas (based on high publications rates or an edited volume) indicated by red lines. The grey shaded area indicates the traditional limits of the savanna biome according to historic sources (White 1983; Beale et al. 2018), although savanna protected areas (i.e., Lamto) sometimes occur outside this boundary.

exert direct influence on tree cover, and that climate, soils, and landscape variables may exert indirect effects on tree cover as mediated by their effects on elephants or fire (e.g., Lehmann et al. 2014).

2 | Methods

2.1 | Creation of the African Database of Savanna Protected Areas (ADSPA)

We downloaded geospatial protected area boundaries (i.e., polygons) from the World Database on Protected Areas (WDPA) and retained all protected areas that intersected the savanna biome layer from Beale et al. (2018; Supporting Information). These included protected areas above 300 mm year^{-1} of precipitation with a heterogeneous tree layer over a grassy herbaceous layer often characterised by the presence of large herbivores and fire. Co-authors with expertise in different regions of Africa (e.g., western, eastern, and southern) then validated the identity of each protected area classified as savanna. Protected areas

dominated by forest vegetation types, or those consisting primarily of mosaics of grassland and forest, were excluded. Recent Google Earth images of each protected area were inspected, and polygon boundaries were modified to exclude recent human encroachment or agriculture. The resulting polygon layer was used to extract environmental variables (see below) and conduct all associated analyses. We refer to the polygon layer, together with the associated ecological and environmental data, as the African Database of Savanna Protected Areas (ADSPA; $n=244$; Figure 1C). This geodatabase can serve as a crucial baseline for future analyses of African savannas to understand global change and human impacts on savanna ecosystems. ADSPA is available for download (Supporting Information; <https://osf.io/xfc67/>) and we welcome edits, improvements and additions as recommended under the Open Science Framework.

2.2 | Primary Literature Search

To understand how research efforts are distributed across African protected savannas, we conducted a primary literature

search using four science library databases: EBSCO, ProQuest, Scopus, and Web of Science. We searched for the name of each savanna protected area from ADSPA and compiled the number of unique instances in which the name occurred in a title or abstract of a scientific publication. We extracted the article title, authors, year, journal name, and abstract from each database, eliminated redundant entries, and counted the number of publications for each protected area ([Supporting Information](#)). Results were visualised with a frequency distribution of the number of publications per park. In addition, we grouped publications by country and clusters (see below) to evaluate how representation in the literature varied spatially (countries) and within functional groupings (clusters).

2.3 | Environmental Variables

For each protected area, we extracted estimates of climate, soils, fire, hydrology, and tree cover from global databases using the *raster* R package (Hijmans 2022). To represent variation in climate across protected areas, we obtained mean annual precipitation (MAP), seasonality (measured as the coefficient of variation in monthly rainfall; SEAS), and mean annual temperature (MAT) from the WorldClim (version 2.1) climate database for 1970–2000 (Fick and Hijmans 2017) at a spatial resolution of 30 arc sec (longitude/latitude), which is ~1 km at the equator. An estimate of the reference evapotranspiration (ET_0) was obtained from the Global Reference Evapotranspiration (Global- ET_0) datasets for the interval of 1970–2000 at a spatial resolution of 30 arc-seconds (Zomer et al. 2022).

To represent soil variation across protected areas we sought variables with well-understood relationships with water, soil fertility, and vegetation. Therefore, we focused on organic carbon (ORGC), percent sand (SAND), and bulk density (BDEN), as these are key predictors of water availability in soils and correlated with indices of soil fertility. We obtained maps of these soil variables at 250 m resolution from the World Soil Information website (ISRIC; Hengl et al. 2015; <https://files.isric.org/public/afsis250m/>). Reflecting our interest in tree cover, we used soil variables estimated to a depth of 15–30 cm (sd3 from the ISRIC database), rather than surface soils, to better represent soil characteristics important to large-scale vegetation patterns.

Wetland extent (WET) was quantified by extracting data from the Global Lakes and Wetlands Database which aggregates the area of 33 lake, river, and wetland classes at a resolution of 15 arc-seconds (Lehner et al. 2024). WET represents the total area (in ha) of each pixel that is lake, river, or wetland (range: 0–21.4 ha). In savannas, wetlands may function as key resource areas for herbivores by providing foraging opportunities during the dry season or by acting as refugia during prolonged drought (Illius and O'Connor 2000). Moreover, seasonally inundated grasslands harbour unique vegetation species composition which makes them distinct from other types of savannas (Fynn et al. 2015). WET was natural log transformed prior to analyses to reduce the right skew resulting from few parks having significant wetland cover.

Topographic variation (TOPO) was quantified by calculating the coefficient of variation (CV) from all elevation values within a

park that were extracted from the digital elevation model (DEM) in the Hydrologic Derivatives for Modelling and Analysis database (Verdin 2017). Prior to analysis, CV DEM values were log transformed to reduce the right skew resulting from high topographic variation in a small number of parks.

To capture potential fire effects on woody cover, we focused on fire intensity, that is, the amount of energy released, and fire frequency. As a proxy for intensity, we generated a fire radiative power (FIRE RAD) layer based on NASA's MODIS satellite available from the Fire Information for Resource Management System (FIRMS; <https://earthdata.nasa.gov/firms>). We utilized the MCD14DL product (61 NRT Hotspot/Active Fire Detections) collected between 2000 and 2015 at a spatial resolution of 1 km and processed the data as described in Hempson et al. (2018). To quantify fire frequency (FIRE FREQ), we counted the number of fires which occurred within a 1×1 km pixel between 2000 and 2019 using the MCD45 MODIS burned area data. This 20-year dataset captures the full range of fire frequencies across protected areas, from those that do not burn to those that burn more than once in some years (Archibald et al. 2010; Staver et al. 2011).

To quantify % woody cover (TREE COVER), we used early 21st century baseline woody cover data at 1 km resolution (Hanan et al. 2020) generated using a combination of optical data from MODIS, with ku-band radar from Q-Scat (Quick Scatterometer), using constrained ensemble Generalised Linear Models informed by 1034 calibration/validation points distributed across African ecosystems (Hanan et al. 2020).

To quantify megaherbivory, we included estimates of historic and recent elephant densities (ELEM) (see below). Unlike other variables, elephant data are not spatially explicit within parks. For each PA we collated all elephant density records from the African elephant database ([Supporting Information](#)), which included elephant density data for 230 parks, and determined the number of unique records (e.g., 1992 census figures might be reported in both the 1995 and 1998 reports). Uniqueness was determined from references provided or, if missing, by eliminating exact matches across years. Historic densities were calculated as the mean density of unique records across all six potential reporting years (1995, 1998, 2002, 2007, 2013, 2016, where we also recorded the number of unique records), and recent densities were calculated as the mean density of unique records across all post-2000 surveys (where we also recorded the number of unique post-2000 survey records). Unfortunately, due to the lack of data for a large enough number of protected areas, we could not include biomass density of all other mammalian savanna herbivores that potentially play a role in savanna vegetation dynamics.

Because of our broad continental focus, all data layers (climate, soil, fire, topography, and hydrology) were aggregated to 5 km² using the 'resample' command in the *raster* package and the center of each raster was extracted for all points that fell within ADSPA polygons. Data layers were transformed to the AFSIS datum prior to extraction to achieve spatial consistency among data layers. The coverage of different data layers permitted the inclusion of 244 savanna protected areas in the analysis of aridity and the remaining environmental analysis.

2.4 | Identification of Groupings With Cluster Analysis

We used Ward's hierarchical cluster analysis (method = "ward.D2" in the 'hclust' command in R) to identify groups of protected areas as defined by soil (BDEN, SAND and ORGC), climate (MAP, ET₀, MAT, SEAS), and landscape features (WET and CV DEM). All variables were equally weighted, scaled to a mean of 0 and a standard deviation of 1 with a distance matrix, then computed using the 'euclidean' distance method in R prior to clustering. We identified the optimal cluster number (range: 2–12) using the 'NbClust' command with the option 'index=all' in the *NbClust* package (Charrad et al. 2014). This function aggregates the results of 30 indices and applies a majority rule, such that the most common cluster number is selected. To understand if clusters represented broader ecological patterns across Africa, we extracted the savanna classification identity, either broad- or fine-leaved savanna, from White's (1983) vegetation map (digitised by Hempson et al. 2019) of Africa for all protected areas and analysed the relative abundance (i.e., area) of each savanna type by cluster. In addition, we used the map of dominant consumer realms from Archibald and Hempson (2016) to classify all pixels as 'high fire', 'high herbivory', 'high fire–high herbivory', or 'low fire – low herbivory'. For both savanna type and consumer realms we used a chi-squared test to test whether the number of observed pixels for each vegetation and consumer type was statistically different from the expected classifications for each of the groups identified from Ward's hierarchical clustering.

To understand within-park environmental variation, we reran a Ward's hierarchical cluster analysis for protected areas that emerged as highly cited from our literature analysis. Our goal was to ask if our analysis of environmental variation could identify recognized and previously documented savanna heterogeneity within well-studied parks in Africa.

2.5 | Quantifying Covariation Among Climate, Soil, Landscape, Fire, Elephants, and Woody Cover

To investigate the direct and indirect associations of climate, soils, topography, and hydrology with fire, elephants, and woody cover in African savannas, we constructed a meta-model (e.g., Grace et al. 2010) based on our understanding of how these processes interact in savannas (e.g., Lehmann et al. 2011; Anderson et al. 2016). Of the 244 parks, we had complete data for 227 which could be included in a multivariate analysis. Our meta-model included direct effects of soil, climate, and landscape variables on fire, elephants and tree cover, and indirect effects of elephants and fire on tree cover. Therefore, our model allowed for the possibility of indirect effects of climate, soils, and landscape variables on tree cover as mediated by their effects on elephants or fire (e.g., Lehmann et al. 2014; Figure S1A). We used the 'psem' command in the R package *piecewiseSEM* (Lefcheck 2016) to first fit a single, biome-wide, structural equation model (SEM) across all savanna protected areas. Path coefficients were extracted with the 'coefs' command and standardized with the option 'standardize = range' (Grace and Bollen 2005). All paths with

$p > 0.05$, including correlations between predictors, were trimmed from our final, accepted model. The coefficients of determination (R^2) for each response variable are based on this final model.

To compare differences among the bioclimatic interactions of clusters, we created a simpler sub-model (Figure S1B) with tree cover as the response variable and fewer predictor variables representing climate (MAP), soil fertility (a composite variable [SOIL] from a principal component analysis of SAND and ORGC), landscape (TOPO), and fire (a composite variable FIRE from a PCA of FIRE FREQ and FIRE RAD), enabling comparison across clusters by promoting model convergence under smaller sample sizes. Like the full metamodel, we assumed that MAP, SOIL, TOPO, and FIRE could have direct effects on TREE COVER, and that MAP, SOIL, and TOPO could have indirect effects on TREE COVER mediated by their direct effects on FIRE. We fit the cluster level data to the sub-model using the same procedures as the full model described above.

3 | Results

3.1 | Primary Literature Search

The literature search yielded 3445 unique publications containing the name of an ADSPA savanna protected area in the title or abstract. Of the 244 parks in the ADSPA search, 94 (38%) were not associated with any peer-reviewed publication in our literature search. South Africa was the most highly represented country in the savanna literature, accounting for 29% of the ADSPA publications from 41 protected areas (Table S1; Figure S2). Zimbabwe ($n = 22$), Zambia ($n = 16$), and Mali ($n = 16$) had numerous protected areas (Table S1) in the database but accounted for just 6%, 3%, and < 1% of the publications, respectively. Two African national parks, Kruger in South Africa ($n = 635$) and Serengeti National Park in Tanzania ($n = 499$), emerged as the most publication-rich savanna protected areas (Figure 1B). The next three publication-rich savanna protected areas were Okavango Delta in Botswana ($n = 173$), Hluhluwe-iMfolozi in South Africa ($n = 168$), and Amboseli National Park in Kenya ($n = 122$); all remaining protected savannas had ≤ 92 publications (Table S2). This means that only 2% of all protected areas (the five above-listed areas) are responsible for 46% of all the savanna science publications we found.

3.2 | Savanna Environmental Variation

ADSPA sites filled nearly the full range of climate space occupied by savannas, but with gaps in arid regions (grey points < 500 MAP and > 2000 ET₀ in the background of Figure 2). ADSPA sites also displayed significant variation in temperature, precipitation seasonality, and in soil variables, such as ORGC, SAND and BDEN (Table 1). WET was strongly right-skewed and ranged from zero to nearly 100% wetland area. The seven well-studied savanna ecosystems (Figure 1; Table 1) represented 76%–100% of the variation in soil parameters and 94% in wetland areas across ADSPA sites, but

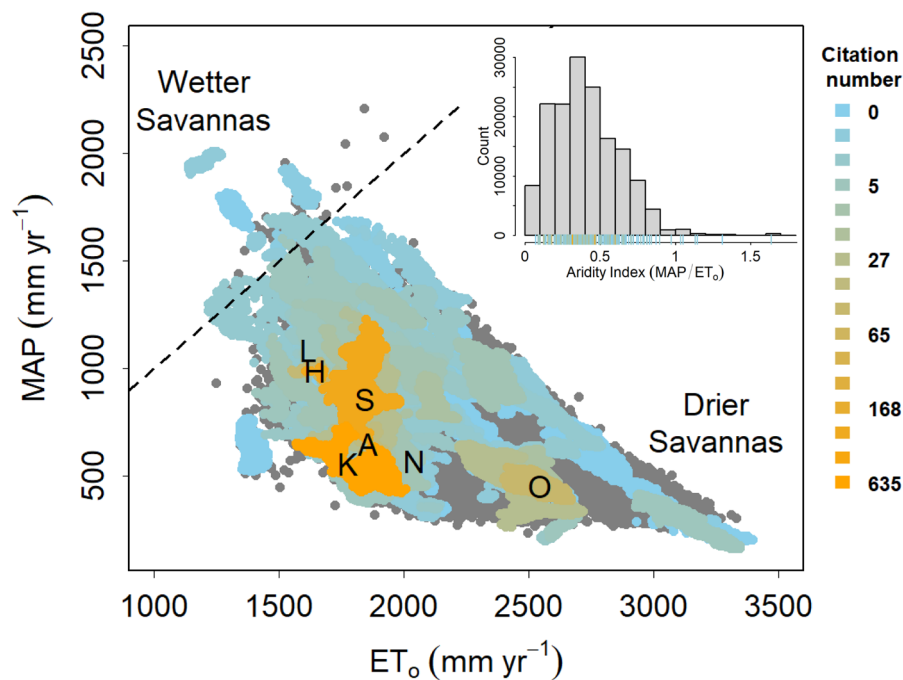


FIGURE 2 | Environmental space for key climatological parameters across African savanna protected areas. The blue to orange points in the foreground are mean reference evapotranspiration (ET_0) plotted against mean annual precipitation (MAP) for each 5 km² pixel in our analysis of 244 African savannas and thus represent existing African protected areas. The dashed line represents the 1:1 line where MAP inputs = ET_0 outputs. The blue to orange colour scale represents the number of publications from Figure 1B, with orange values representing areas with more literature publications (range: Light blue = 0 to orange = 635). The grey points in the background are the same values extracted from a 5 km² grid within the savanna boundary (i.e., the grey shaded area from Figure 1C). Mean values for the seven well-studied areas identified in Figure 1C are shown as letters (A = Amboseli National Park, H = Hluhluwe-iMfolozi Park, K = Kruger National Park, L = Lamto Scientific Reserve, N = Nylsvley Nature Reserve, O = Okavango Delta, and S = Serengeti National Park). Inset figure is the histogram of the aridity index across all protected areas (MAP/ ET_0) with the coloured lines showing the corresponding values for the well-studied areas. Because Lamto station is not a protected area in the ADSPA database, we extracted environmental variables from the nearest protected savanna park (~68 km N of Lamto).

TABLE 1 | Range of values for climate, soil, and landscape variables across the African savanna biome, areas within the African Database of Savanna Protected Areas (ADSPA) and from seven well-studied savanna areas (Figure 1C).

Type	Variable	Savanna biome range	ADSPA range	Seven well-studied areas	Proportion of ADSPA
Climate	MAP	236.1–2207.6 mm year ⁻¹	160.2–2008.3 mm year ⁻¹	385.8–1227.5 mm year ⁻¹	0.46
	ET_0	1246–3329 mm year ⁻¹	1136–3394 mm year ⁻¹	1551.7–2667.5 mm year ⁻¹	0.49
	Aridity	0.08–1.29	0.05–1.71	0.15–0.68	0.32
	MAT	7.2°C–30.4°C	13.4°C–30.2°C	18.0°C–26.7°C	0.52
	SEAS	24.8–170.1	24.3–159.2	40.6–113.7	0.54
Soil	BDEN	1010–1870 kg dm ⁻³	1016.8–1725.8 kg dm ⁻³	1016.8–1554.9 kg dm ⁻³	0.76
	ORGC	0–62 g kg ⁻¹	0–58.1 g kg ⁻¹	0–58.1 g kg ⁻¹	1.0
	SAND	0%–93%	22.2%–93.7%	24.7%–89.8%	0.91
Landscape	DEM	0–3004 m	3–2399 m	69–1980 m	0.80
	WET	0–21.4	0–21.4	0–20.3	0.94

Note: All values are extracted from GIS layers represented at a resolution of 5 km. Proportion of ADSPA represents the amount of the ADSPA range accounted for by the range of the seven well-studied areas (i.e., seven area range/ADSPA range). ADSPA values fall outside the range of the savanna biome values when a protected area classified as a savanna is located outside the savanna biome as defined by the literature (see Figure 1). Aridity: MAP/ ET_0 . Abbreviations: BDEN, bulk density (kg dm⁻³); DEM, digital elevation model (m); ET_0 , evapotranspiration (mm year⁻¹); MAP, mean annual precipitation (mm year⁻¹); MAT, mean annual temperature (°C); ORGC, organic carbon (g kg⁻¹); SAND, sand (%); SEAS, seasonality; WET, wetland area per pixel (ha).

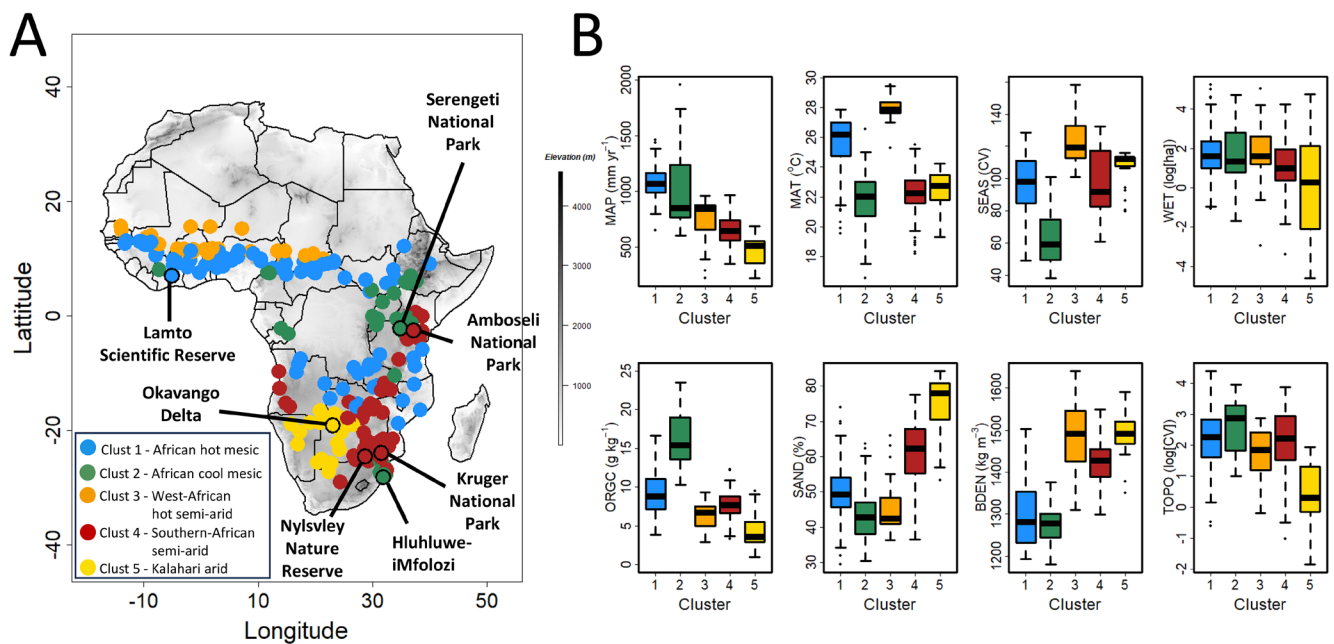


FIGURE 3 | (A) A map of Africa showing each savanna protected area as one of five possible savanna clusters grouped according to climate, soil, and landscape parameters (see Section 2; Figure S4). (B) Boxplots of the mean annual precipitation (MAP), mean annual temperature (MAT), seasonality of precipitation (SEAS), natural log of wetland area (WET), soil organic carbon (ORGC), soil percent sand (SAND), soil bulk density (BDEN), and natural log of the coefficient of variation in elevation (TOPO) for each protected savanna grouped according to the five savanna cluster types shown in (A). Elevation is displayed over the map of Africa to highlight the that separation of the continent into “High Africa” in the south and east and “Low Africa” in the north and west (White 1983).

just 32%–54% in climate parameters. The seven well-studied savannas tend to occur in regions of relatively low MAP ($< 1000 \text{ mm year}^{-1}$) and, except for the Okavango Delta, intermediate to low ET_0 ($< 2000 \text{ mm year}^{-1}$; Figure 2).

3.3 | Cluster Results

Cluster analysis based on climate, soils, and landscape variables identified $k = 5$ as the optimum cluster number for African protected savannas (Figure 3A; Figure S4A), which we have chosen to order by rainfall. Cluster 1, *African hot mesic savannas* ($n = 83$; 34% of savannas) included savannas with high MAP and MAT, moderate SEAS and low soil BDEN. African hot mesic savannas are represented by parks such as Comoe (CIV), Gorongosa (MOZ), Lamto (CIV), Liuwa Plain (ZAM), Mole (GHA), Niassa (MOZ), and Selous–Nyerere (TAN), and have low representation in the peer-reviewed literature (14.5%; $n = 498$).

Cluster 2, *African cool mesic fertile savannas* ($n = 34$; 14% of savannas), grouped widely scattered savannas with high MAP, the lowest SEAS, and soils with the highest ORGC and lowest BDEN, likely because of volcanic origins (Figure 3). African cool mesic fertile savannas were well represented in the peer-reviewed literature (28.1%; $n = 968$) including well-studied parks such as Hluhluwe-iMfolozi (ZAF), Lake Nakuru (KEN), Masai Mara (KEN), Nairobi (KEN), Omo (ETH), Queen Elizabeth (UGA), and Serengeti (TAN).

Cluster 3, *West-African hot semi-arid savannas* ($n = 26$; 11% of savannas), grouped areas with high MAT and SEAS, soils of high BDEN and low ORGC, stretching in a west to east band across

the Sudanian savanna and southern Sahelian regions of west Africa (Figure 3). West-African hot semi-arid savannas were the least represented savannas in the peer-reviewed literature (2.1%; $n = 72$).

Cluster 4, *Southern-African semi-arid savannas* ($n = 73$; 30% of savannas) grouped parks across east and southern Africa (Figure 3A), and with intermediate environmental variation in all the variables we studied (Figure 3B). Southern-African semi-arid savannas were best represented in the peer-reviewed literature (39%; $n = 1342$) consisting of ‘classic’ savanna protected areas such as Amboseli (KEN), Kafue (ZMB), Kruger (ZAF), Luangwa (ZMB), Tarangire (TAN), Tsavo (KEN), and Zambezi (ZAF).

Cluster 5, *Kalahari arid savannas* ($n = 28$; 12% of savannas), grouped the low MAP, low CV DEM (i.e., flat), and high SAND savannas centered around the Kalahari basin in Botswana, Namibia, South Africa, and Zimbabwe (Figure 3). Kalahari arid savannas account for 16.3% of peer-reviewed publications ($n = 559$). Despite including well-known wetland systems such as Okavango (BWA) and Chobe (BWA), the cluster also included many protected areas with low proportions of wetland surface area such as Kalahari (BWE) and Hwange (ZWE; Figure 3B).

To explore within-savanna heterogeneity, we reran a Ward’s hierarchical cluster analysis for the four ecosystems with > 150 publications (i.e., Kruger, Serengeti, Okavango, and Hluhluwe-iMfolozi) using the 5 km resolution climate, soil, and landscape variables data as inputs. These four well-studied savannas had $k \geq 3$ cluster types within their boundaries. Cluster distributions aligned with ecological boundaries within the parks (Figure S3),

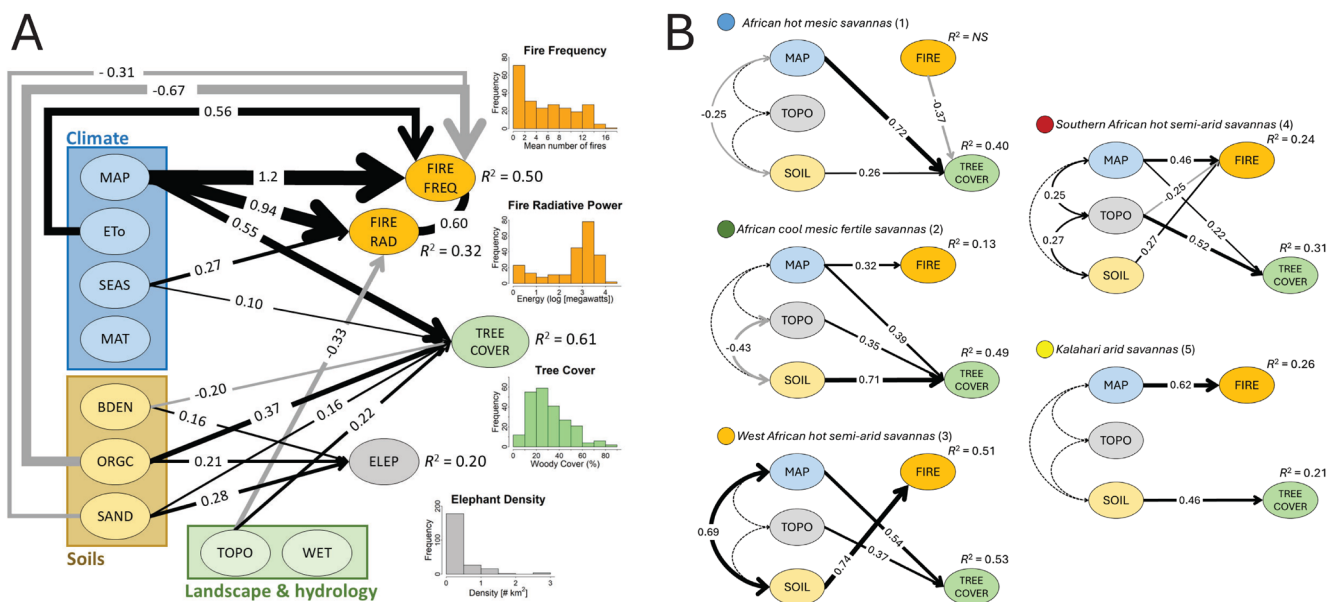


FIGURE 4 | (A) Final structural equation (SE) model results for all areas in the ADSPA dataset ($n=227$). Abiotic predictors are grouped into climate (mean annual precipitation = MAP; annual evapotranspiration = E_{TO} ; climate seasonality = SEAS; mean annual temperature = MAT), soils (bulk density = BDEN; organic carbon = ORGC; percent sand = SAND), and landscape (log coefficient of variation in digital elevation = TOPO) and hydrology (log wetland area = WET). Response variables were fire frequency (FIRE FREQ), fire radiative power (FIRE RAD), elephant densities (ELEP), and percent tree cover (TREE COVER). Histograms of the response variables and their coefficients of determination (R^2) within each savanna cluster are displayed adjacent to the variable name. Statistically significant direct effects are displayed as straight arrows with thickness indicating effect strength and colour indicating sign (positive = black; negative = grey). The correlation coefficients between FIRE FREQ and FIRE RAD are displayed adjacent to the solid curved lines, with the strength of the correlation proportional to line thickness. Other predictor variables were allowed to covary, but for simplicity these relationships are not shown. Standardised and unstandardized effects for the full model are in Table S3. (B) Final SE models for the five individual clusters. Cluster models included fewer variables than the full model so that results were conceptually tractable and because of smaller sample sizes associated with subsetting the data by cluster (see Section 2). Arrow line type, thickness, and colours are as in (A). Standardised and unstandardized effects for the cluster results are in Table S4.

including soil type differences in Kruger and broad vegetation differences in Serengeti.

Across the entire biome, TREE COVER showed a significant linear relationship with MAP ($F_{1,240}=209.0$, $\beta_{\text{TREE COVER}} \pm \text{SE} = 0.04 \pm 0.003$, $p < 0.001$, $R^2 = 0.46$; Figure S4C). Mean TREE COVER ($\pm \text{SD}$) was tightly associated with MAP across clusters, except for West-African hot semi-arid savannas in the Sahel, which had lower than expected TREE COVER based on MAP (Figure S4B): cluster 1 (African hot mesic savannas) = $41.7\% \pm 15.2\%$, cluster 2 (African cool mesic fertile savannas) = $40.2\% \pm 18.0\%$, cluster 3 (West-African hot semi-arid savannas) = $17.5\% \pm 8.0\%$, cluster 4 (Southern-African semi-arid savannas) = $26.0\% \pm 7.9\%$, and cluster 5 (Kalahari arid savannas) = $16.1\% \pm 6.1\%$. Within clusters there were significant positive relationships between TREE COVER and MAP, except for Kalahari arid savannas, in which there was no statistical evidence for a positive relationship (Figure S4C).

Observed extent of broad-leaved versus fine-leaved savannas differed across clusters ($\chi^2 = 60.7$, $\text{df} = 4$, $p < 0.001$) and was consistent with broad patterns of savanna vegetation well established for Africa. African hot mesic savannas were characterised by greater broad- compared to fine-leaved systems (fine_{Clust1}:broad_{Clust1} = 23:52). Southern-African semi-arid savannas were equally balanced between fine- and broad-leaved savannas (fine_{Clust4}:broad_{Clust4} = 36:34). The remaining three

clusters, which cover a wide range of soil properties, including nutrient-rich (African cool mesic fertile savannas) and sandy (Kalahari arid savannas), were similar in that they were disproportionately characterised by fine- compared to broad-leaved savannas (fine_{Clust2}:broad_{Clust2} = 24:2; fine_{Clust3}:broad_{Clust3} = 23:2; fine_{Clust5}:broad_{Clust5} = 23:2).

All clusters included significant areas with 'consumer' regimes classified as both high fire and high herbivory as defined by Archibald and Hempson (2016). African hot mesic savannas (cluster 1) and Kalahari arid savannas (cluster 5) included large high fire regions, while African cool mesic fertile savannas (cluster 2) and Southern African semi-arid savannas (cluster 4) included extensive high herbivory regions. Kalahari arid savannas were unique in containing areas with both low fire and low herbivory (Figure S5).

3.4 | Structural Equation Model Analysis of Woody Cover

Our SE modelling approach estimated direct and indirect effects of climate, soils, and landscape features on fire, elephant abundance, and woody cover in African savannas (Figure 4A; Table S3), and sub-model analyses revealed differences in ecological and environmental relationships among savanna clusters (Figure 4B; Table S4). Coefficients of determination (R^2)

for the full metamodel ranged from 0.20 for ELEP to 0.61 for TREE COVER. Several important results emerged from the SE modelling. First, MAP was the strongest direct driver of TREE COVER (0.55), FIRE FREQ (1.2), and FIRE RAD (0.94) at the scale of the entire ADSPA dataset (Figure 4A). Second, FIRE RAD and FIRE FREQ were strongly correlated (0.60), but direct effects of fire on TREE COVER were not significant within the context of our model. Third, soils and landscape variables had prominent associations with TREE cover, including positive effects from ORGC (0.37), SAND (0.16), and TOPO (0.22) and negative effects of BDEN (−0.20). Finally, soils also had significant positive effects on ELEP, and after accounting for these effects there was no significant relationship between TREE COVER and ELEP.

The SE models of the individual clusters revealed key similarities and differences in savanna function across savannas and regions. TREE COVER increased with MAP in all clusters except in the Kalahari arid savannas (cluster 5; Table S4). Likewise, TREE COVER increased with TOPO in African cool mesic fertile savannas (cluster 2; 0.35), West-African hot semi-arid savannas (0.37), and Southern-African semi-arid savannas (cluster 4; 0.52). TREE COVER increased with SOIL (an index of soil fertility, with SOIL positively related to ORGC and negatively related to SAND) in African hot mesic savannas (cluster 1; 0.26), African cool mesic fertile savannas (cluster 2; 0.71), and Kalahari arid savannas (cluster 5; 0.46). However, relationships between MAP and FIRE and between FIRE and TREE COVER differed among clusters. In African hot mesic savannas (cluster 1), MAP had no statistical relationship to FIRE, but FIRE had a relatively strong negative effect on TREE COVER (−0.37). MAP was positively related to FIRE in African cool mesic fertile savannas (cluster 2; 0.32), Southern-African semi-arid savannas (cluster 4; 0.46), and Kalahari arid savannas (cluster 5; 0.62), whereas in West-African hot semi-arid savannas (cluster 3) SOIL was positively related to FIRE (0.74); however these did not translate into FIRE effects on TREE COVER.

4 | Discussion

Our analysis identified five savanna groupings in Africa, based on variation in climate, soil, and landscape variation across savanna protected areas, which differ from previous delimitations based on floristic data. For example, biogeographic analyses of savanna woody plant species by Fayolle et al. (2019) divided Africa into eight regional clusters nested within two broad groups, one in lower elevation northwestern Africa and the other in higher elevation southeastern Africa. Gorel et al. (2022) investigated niche lability across African biomes and identified two climatic groups of savannas: the ‘hot savannas’ spanning the Sahel in West Africa and ‘cold savannas’ which span Ethiopia, through eastern Africa, down to South Africa.

The ‘cold savannas’ grouping of Gorel et al. (2022) aligns with our African cool mesic fertile savannas (cluster 2), Southern-African semi-arid savannas (cluster 4), and Kalahari arid savannas (cluster 5), while their ‘hot, seasonal savannas’ align with our African hot mesic savannas (cluster 1) and West-African hot semi-arid savannas (cluster 3). However, our dataset extends

further into southern Africa and unlike Gorel et al. (2022) our analysis includes soil and landscape variation. Soils differentiate our three cool savanna groups: the Kalahari savannas are infertile and sandy, eastern and southern African savannas have intermediate fertility, and the savannas surrounding the Congo basin are fertile, often associated with volcanic soils arising from uplift and the Great Rift Valley. Moreover, soils also differentiate western African hot savannas into lower fertility, high bulk-density Sahelian savannas and higher fertility, low bulk-density coastal savannas (Figure 3).

Overall, taxonomic (Osborne et al. 2018; Fayolle et al. 2019; Gorel et al. 2022), climate (Gorel et al. 2022 and this study), and soils-based analyses (this study) of savanna groupings suggest that distinct hot, seasonal savannas are widespread in West Africa (clusters 1 and 3), around the Congo basin, and in a large swath of lowland areas in Mozambique and Tanzania (cluster 1; Figure 3). However, as revealed by our literature search of the ADSPA sites, these are relatively understudied savannas (but see Couteron and Kokou 1997; Ribeiro et al. 2008; Hiernaux et al. 2009; Seghieri et al. 2009; Miede et al. 2010; Brandt et al. 2016, among others). The hot conditions in these ecosystems may have important consequences for savanna structure and function, including by increasing fire frequency and intensity (e.g., Hempson et al. 2018; Figure 4B). Thermal conditions also control savanna structure and function through direct effects on phenology and stem elongation (e.g., Chidumayo 2001) and via indirect effects on plant functional types (e.g., Skarpe 1996) and thereby on disturbance regimes (Osborne et al. 2018). In a modelling study focused at the continental scale, Boone et al. (2018) predicted that future climate change will erode the capacity of the West-African region to produce herbaceous biomass, and yet these predictions are unexamined in the field.

Although our clusters only weakly align with taxonomic delineations, our savanna clusters are consistent with tree functional groupings based on leaf type, that is, those dominated by fine-leaved versus mixtures of broad- and fine-leaved trees (Huntley 1982; Hempson et al. 2019). This finding is consistent with the hypothesis that environmental drivers explain broad patterns of conservatism in vegetation traits within regions of climatic similarity (e.g., Conradi et al. 2020), and that niche conservatism is seen at the biome scale more broadly (e.g., Crisp et al. 2009).

While our groupings reveal broad continental patterns and illuminate differences among savannas across Africa, these generalisations mask significant variation within ecosystems. Our cluster analysis did not consider protected area size or within-ecosystem heterogeneity, but instead inferred group membership based on mean values from an entire protected area. For large or heterogeneous ecosystems, this may obscure ecologically important gradients. For example, Southern African semi-arid savanna, which was equally distributed between fine- and broad-leaved woody savannas, included the well-studied ecosystems of Kruger NP and Amboseli NP as well as Luangwa, Tsavo, and Zambezi. Each of these protected areas harbours within-park habitat variation. For example, Kruger is well known to include both basaltic and granitic soils in the east and west, respectively (e.g., Smit et al. 2013) and *acacia*- and dwarf *mopane-dominated vegetation* in the south vs. north

respectively (e.g., Stevens 2021). Likewise, African cool mesic fertile savannas are associated with fine-leaved woody savannas, represented by the well-studied Hluhluwe-iMfolozi and Serengeti. These protected areas are similar in having relatively fertile soils and high rainfall but incorporate substantial vegetation heterogeneity and rainfall gradients. Serengeti, for example, comprises open grasslands, fine-leaved *Vachellia* and *Senegalia* (formerly *Acacia*)-*Commiphora* woodlands, and broad-leaved, miombo-like woodland vegetation in the high rainfall north-west part of the park (Jager 1982; Herlocker 1974). Likewise, Hluhluwe-iMfolozi ranges from broad-leaved woodland savannas in the more mesic north to more open, parkland, fine-leaved savannas in the semi-arid south (Cromsigt et al. 2017). Our within-protected area cluster analysis (Figure S3) suggests that incorporating savanna variability may be an interesting and overlooked characteristic by which to group savannas in the future (e.g., Du Toit et al. 2003).

Our focus on well-studied and highly cited ecosystems is meant to illuminate gaps in savanna research across the continent, not to provide an exhaustive assessment of African savanna research. There are examples of other well-studied savannas not included in our list of seven 'well-studied' systems (e.g., Figure 1) that have contributed significantly to savanna research. Two notable examples are Mpala Research Centre, and other sites in Laikipia, in Kenya and Gorongosa National Park in Mozambique. Long-term research at Mpala is shaping our understanding of plant-herbivore interactions, especially by experimentally teasing apart the effects of wild herbivores ranging from small mammals to mega herbivores and even livestock (Goheen et al. 2010; Kimuyu et al. 2017; Goheen et al. 2018; Young et al. 2018; Riginos et al. 2018). Mpala consists of two major habitats including a dry, 'red-sand' habitat similar to Southern-African semi-arid savannas (Augustine 2003), and a black-cotton *Vachellia* (formerly *Acacia*) *drepanolobium* woodland similar to African cool mesic fertile savannas (Riginos and Grace 2008). Work in Gorongosa, grouped with African hot mesic savannas, is elucidating how animal communities reassemble after human-caused decline (i.e., Daskin et al. 2016; Pansu et al. 2019; Stalmans et al. 2019; Gaynor et al. 2021). Other examples of systems that did not make our 'well-studied' list include the Katavi-Rukwa ecosystem in Tanzania (e.g., Mulder et al. 2007), Niassa Special Reserve in Mozambique (Ribeiro et al. 2008), and Luambe National Park and South Luangwa in Zambia (Creel et al. 2019). Research in rangelands has also made considerable contributions to our understanding of savanna ecosystems but is not considered here due to the difficulty of reconciling the wide range of potential management interventions across rangeland study areas. Excluding these areas may distort our assessment of research effort by savanna groupings, although we suspect the socioeconomic factors that drive research imbalances among protected areas also apply to research in rangelands. Finally, research being conducted by the Socio-Ecological Observatory for Studying African Woodlands (SEOSAW) is filling gaps throughout southern and eastern African savannas and (mostly) miombo woodlands (e.g., Godlee et al. 2021; Davies et al. 2023). Species compositional and community structure data have been collected across ~10,000 plots and 12 countries (SEOSAW Partnership 2021) and are opening new avenues of research based on plant species compositional data.

Our findings suggest that protected areas in the West-African hot semi-arid savannas (Figure 3) remain the least understood savannas in Africa and are without representation of long-term research programs focused on the controls of savanna structure and function. That is not to say that this cluster is completely unstudied, because long-term research in West Africa has focused on plant phenology as a driver of (and responsive to) flammability and fire dynamics (Menaut and Cesar 1982; De Bie et al. 1998). However, future climate change scenarios predict strong effects on rangeland vegetation in this region of West Africa (Boone et al. 2018). Thus, the results of our analysis, together with climate change predictions, suggest that savannas within this cluster are understudied.

Like previous analyses across continents (e.g., Lehmann et al. 2014), our analysis has revealed differences in the relationships among climate, soils, landscape variation, fire, and woody cover across African savannas. Biomass consumption pathways, described as fire- versus herbivory-dominated by Archibald and Hempson (2016), varied by cluster. African cool mesic fertile savannas and Southern-African semi-arid savannas are dominated by herbivory (Figure S4), perhaps accounting for the lack of a significant FIRE effect on TREE COVER in the former. By contrast, at intermediate to high rainfall (i.e., Hempson et al. 2018), fire is expected to dominate consumption, which is consistent with our finding that FIRE was most negatively associated with TREE COVER in the African hot mesic savannas. Furthermore, the finding that FIRE was not significantly related to MAP in this cluster suggests that rainfall does not limit the production of fuel as it does in other savanna regions. Our results, that FIRE was not significantly associated with TREE COVER across four clusters, and therefore significant parts of the African savanna biome, may seem surprising at first, but they are consistent with previous research in African savannas that showed that tree density can be relatively unresponsive to fire return interval in some climate envelopes (Higgins et al. 2007).

Our SE models were unable to explain variation in elephant densities, which is not surprising. Firstly, African elephants have large dispersal distances, and thus there is reason to believe that populations in southern and eastern Africa have been connected over the past 4 million years (e.g., Georgiadis et al. 1994). But more importantly, while past densities may have been predictable by climate, soil, and vegetation parameters, elephant populations are declining in most countries, and overall, current elephant populations are not representative of even recent historic abundance (Chase et al. 2016; Hauenstein et al. 2019). Our inclusion of these data in ADSPA is meant to provide data with the potential to be linked to the monitoring and management of elephants within savanna protected areas.

The consumer realms provide insight into herbivore variation among clusters, yet our study lacks a direct measure of grazing and browsing herbivores, which play key roles in structuring vegetation in the drier African savannas (i.e., 400–800 mm year⁻¹, Staver et al. 2021). While many protected areas included in this study have good elephant abundance data, this was not the case for most other herbivore populations. Future work may elucidate controls on herbivore communities across these ecosystems and their contributions to structuring savanna vegetation. While

the historic functional type differences of herbivores at broad scales are known across Africa (e.g., Hempson et al. 2015), our study stresses a need for more detailed, spatially explicit, data on the biomass density of all savanna herbivores across African protected areas to assess their role in savanna ecosystem functioning. In addition, our study deliberately focused on protected areas to control for the direct effects of human-driven land cover change and human influence on ecological patterns and processes. We acknowledge, however, humans have been integral to African savannas for millennia and remain key drivers of these systems. While beyond the scope of this study, future research should examine how human activities shape ecological dynamics differently across Africa, depending on cultural, environmental, and socio-economic contexts.

5 | Conclusion

We offer a new database of protected African savannas (ADSPA) emphasizing multiple environmental variables. We analyzed variation in tree cover, fire, and elephants with respect to climate, soils, fire, elephant and landscape variables. We argue that there is an urgent need to understand the functionality of African savanna ecosystems and the key drivers of tree cover, given the highly threatened status of African savannas and the animals that depend on them.

By comparing across systems and identifying gaps between well-studied protected areas, we hope to dispel misconceptions that have arisen because of research focused in a relatively restricted area of the savanna niche space. For example, understanding tree-grass ratios has absorbed years of research efforts and focused on sites with different drivers (Holdo and Nippert 2022). It is our hope that the ADSPA will provide a baseline for environmental monitoring and yield data to deepen our understanding of savannas across Africa, especially in the understudied protected areas of West Africa. Protected areas are facing mounting ecological risks due to climate change and expanding human populations at the boundaries of savanna protected areas—we hope ADSPA will serve as a tool to address these risks.

Author Contributions

T.M.A., G.P.H., J.E.D., C.M.B., M.T.B., C.C.-M., J.P.G.M.C., R.F., C.L.P., J.P., I.P.J.S., A.C.S., and S.A. conceived of the idea. All authors contributed to the assembly and validation of ADSPA. S.A. processed the fire data. C.F. constructed and ran the literature search. N.P.H. created the woody cover layer. T.M.A., G.P.H. and J.E.D. assembled and processed the data. T.M.A. analyzed the data and wrote the first draft of the manuscript. All authors contributed to the editing and writing of the manuscript.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

Upon acceptance all data, metadata, Supporting Information, and R scripts will be made available through Dryad (<https://doi.org/10.5061/dryad.9ghx3ffxp>) the Open Science Framework platform (<https://osf.io/xfc67/>) thus promoting data sharing and collaboration.

Peer Review

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Data S1:** ddi70123-sup-0001-DataS1.zip.